
REVISION OF PALEOTROPICAL *MEGALASTRUM* (DRYOPTERIDACEAE)¹

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ABSTRACT

We recognize three species of *Megalastrum* Holttum (Dryopteridaceae) in Africa, the Comoros, Madagascar, Mauritius, and La Réunion. A key to distinguish the three species is provided as well as description, complete synonymy, discussion, specimens examined, and illustration of each species. Two names are excluded from the genus.

Key words: Africa, Comoros, Dryopteridaceae, ferns, Indian Ocean, Madagascar, Mascarene Islands, *Megalastrum*, pteridophytes, systematics, taxonomy.

This paper treats the species of *Megalastrum* Holttum (Dryopteridaceae) occurring in continental Africa, the Comoros, Madagascar, Mauritius, and La Réunion. These are the only areas where the genus is known in the Paleotropics. We estimate that *Megalastrum* contains about 83 species worldwide, some as yet undescribed. The present work is the fifth in a series of papers treating the genus in large geographic regions. The four previous articles published in this series are treatments of the 18 species of *Megalastrum* in Brazil, Paraguay, and Uruguay (Moran et al., 2009a), the nine species in the West Indies (Moran et al., 2009b), the 21 species in Central America (Moran & Prado, 2010), and the seven species in the circumaustral region (Sundue et al., 2010). A separate treatment is underway for South America. Between any two of these regions there is little or no geographic overlap of species.

For a review of the taxonomic history and geography of *Megalastrum*, see Smith and Moran (1987) and Moran et al. (2009a). Christensen (1913, 1920) was the first to point out the distinctiveness of the group. He noted its characteristic laminar cutting and venation; namely, as one goes distally along the pinna, the basal basiscopic pinnules gradually become decurrent and broadly adnate to the pinna rachis. Correspondingly, the vein that supplies the broadly adnate segment or lobe arises from the pinna

rachis, not the costule. Among ferns, this combined cutting and venation pattern is noteworthy. Christensen (1913, 1920) pointed out that the form of the hairs on the adaxial surfaces of pinna rachises was a helpful characteristic in identification. Generally, these hairs are coarse, whitish, septate, acicular, and antrorsely or patently strigose (Smith & Moran, 1987). After drying, they often remain terete, the cells not collapsing and twisting at right angles to each other (also observed in the genus *Ctenitis* (C. Chr.) C. Chr.). A distinctive character of *Megalastrum* is that the veins in almost all species end before the laminar margins in enlarged tips (hydathodes). This type of vein termination is uncommon among dryopteroid ferns, which typically have slender vein tips that reach the margin. The Paleotropical *M. lanuginosum* (Willd. ex Kaulf.) Holttum is atypical in the genus by having slender vein tips that extend near or all the way to the laminar margin.

The above characteristics were first pointed out by Christensen (1913: 82–84, 1920: 31–32, 59–60), who treated the species now classified in *Megalastrum* as the “group of *D. [Dryopteris] subincisa*” of subgenus *Ctenitis* C. Chr. in *Dryopteris* Adans. He assigned about 30 Neotropical species to the group but did not treat the Paleotropical species. Holttum (1983) published a study of *Ctenitis* for the Mascarene Islands, distinguishing three species in

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section *Subincisae* (C. Chr.) Tindale (*C. lanuginosa* (Willd. ex Kaulf.) Copel., *C. canacae* Holttum, and *C. lanata* (Fée) Holttum), but without citing any specimens. Later, Holttum published *Megalastrum* as a new genus (1986), recognizing five Paleotropical species (no infraspecific taxa), but he did not provide a treatment for them (no key or descriptions). Since Holttum's work, no further comprehensive study has been published for the Paleotropical species of *Megalastrum*.

The purpose of our study was to review the species of *Megalastrum* throughout Africa and the western Indian Ocean region, to examine relevant types, and to provide a new taxonomic treatment.

MATERIAL AND METHODS

Herbarium specimens were requested on loan from 16 herbaria: AAU, B, BOL, BR, GH, HBG, K, MICH, MO, NBG, NY, P, PRE, S, US, and WAG. A complete listing of voucher specimens is provided in Appendix 1. To produce the distribution map, the geographic coordinates had to be estimated for most of the specimens because this information was not provided on most labels. Our estimates of geographic coordinates are given in brackets in the Specimens Examined section. The dot distribution map was generated in the geographic information system (GIS) laboratory at the New York Botanical Garden.

RESULTS

Three species, with no infraspecific taxa, are here recognized for the Paleotropics. The first species, *Megalastrum lanuginosum*, has the widest distribution (Fig. 1). The distribution is disjunct in three areas: (1) the western Indian Ocean area (Madagascar, the Comoros, La Réunion, and Mauritius), (2) southern and eastern Africa, and (3) the islands of the Gulf of Guinea in western Africa (Bioko and São Tomé). Similar disjunctions are known for other ferns like *Grammitis nigrocincta* Alston, *Trichomanes digitatum* Sw., and *Antrophyum immersum* (Bory ex Willd.) Hook. & Baker (Figueiredo & Gascoigne, 2001). The two other species, *M. canacae* (Holttum) Holttum and *M. lanatum* (Fée) Holttum, are narrow endemics, occurring only in the Mascarene Islands (La Réunion and Mauritius) and in La Réunion, respectively.

According to preliminary results of molecular phylogeny (unpublished data), the two endemic species to the Mascarene Islands (*Megalastrum canacae* and *M. lanatum*) constitute a clade that is sister to the rest of the genus. Both species share fenestrate perispores, a character unique in the genus

(pers. obs.). In contrast, *M. lanuginosum* belongs to a clade of Brazilian species and was resolved sister lineage to *M. crenulans* (Fée) A. R. Sm. & R. C. Moran. The two species share three characters that are rare elsewhere in the genus: bullate scales on the lamina axes, indusiate sori, and veins that extend to the margins (or nearly so) and are nonhydathodous.

Megalastrum Holttum, Gard. Bull. Singapore 39: 161. 1986. TYPE: *Megalastrum villosum* (L.) Holttum [= *Polypodium villosum* L.].

Dryopteris Adans. subg. *Ctenitis* C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Math. Afd. ser. 8, 6: 32, 59. 1919 [1920], as "restricted to the species group of *D. subincisa* C. Chr."

Dryopteris sect. *Subincisae* C. Chr., Index Fil., Suppl. 3, 7. 1934. *Ctenitis* C. Chr. sect. *Subincisae* (C. Chr.) Tindale, Contr. New South Wales Natl. Herb. 3: 252. 1965. TYPE: *Dryopteris subincisa* (Willd.) Urb., 1903 [= *Polypodium subincisum* Willd., 1810].

Plants terrestrial; rhizomes erect to decumbent; petioles scaly toward the base, with 4 to 10 vascular bundles, the 2 adaxial bundles enlarged; laminae 1-pinnate-pinnatifid ranging to 4-pinnate-pinnatifid, catadromic above the basal pinnae; basal pinnae inequilateral and enlarged on the basiscopic side or (less commonly) equilateral; rachises, pinna rachises, and costules not grooved or only shallowly so, scaly and pubescent abaxially, densely pubescent on the adaxial surfaces, the hairs whitish, spreading to antrorsely strigose, multicellular, if glands present, these ca. 0.1 mm wide, spherical, shiny, yellowish to orangish clear, sessile to stalked; basal basiscopic segment of pinnules becoming decurrent and adnate to the pinna rachises, the vein supplying the segment springing from the pinna rachis instead of the costule; hydathodes present or (more rarely) absent; indusia absent or (less commonly) present, circular, brown, firm, in some species minute and fugacious; spores monolete, nongreen, the perispores cristate or spiny, nonfenestrate or rarely so (2 species); $x = 41$ (Kramer & Green, 1990).

Etymology. The name *Megalastrum* is taken from the Greek "mega-," meaning "large," and "-*Lastrea*," which refers to the genus *Lastrea* Bory named after the French botanist Charles Jean Louis Delastre (1792–1859). When *Ctenitis* was first published (as a subgenus of *Dryopteris*), it included species now placed in *Ctenitis*, *Megalastrum*, and *Triplophyllum* Holttum. Christensen later (1919) recognized four informal species groups within the subgenus, one of which he called the "Group of *D. subincisa*." This group is the same as what we are calling *Megalastrum*.

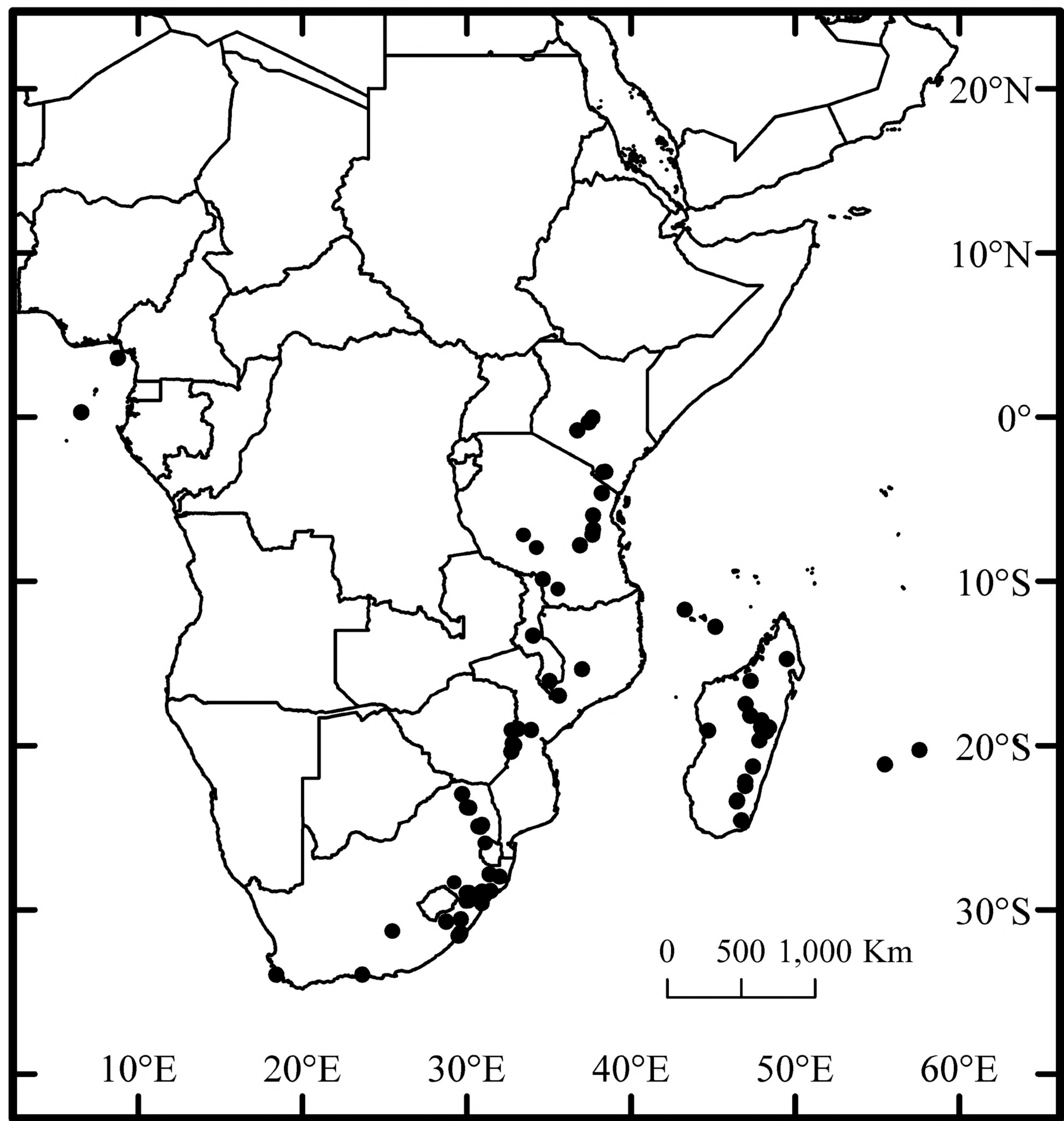


Figure 1. Disjunct distribution of *Megalastrum lanuginosum* between tropical West Africa, where restricted to Bioko and São Tomé, and the eastern Africa and Madagascan region. Black dots indicate the vouchered occurrence of the species.

KEY TO THE SPECIES OF *MEGALASTRUM* IN AFRICA, MADAGASCAR, THE COMOROS, LA RÉUNION, AND MAURITIUS

- 1a. Rhizome scales golden brown, denticulate; laminae tripinnate-pinnatifid or more divided at the base; indusia conspicuous and persistent, large, to 1.5 mm diam.; bullate scales sparse to abundant on costules and smaller axes abaxially 3. *M. lanuginosum*
- 1b. Rhizome scales dark brown, subentire; laminae bipinnate-pinnatisect or less divided at base; indusia 0.3–0.5 mm diam. or absent; bullate scales absent on costules and lesser axes.
 - 2a. Lamina on both surfaces between veins glabrous; indusia persistent; hairs of the pinna rachises 0.2–0.5 mm long on the abaxial surfaces, 0.8–1.2 mm long on the adaxial surfaces; hairs of the abaxial surfaces of costules 0.1–0.4 mm long 1. *M. canacae*
 - 2b. Lamina on both surfaces between veins pubescent; indusia absent (rarely present and if so, fugacious); hairs of the pinna rachises 0.5–1.2 mm long on the abaxial surfaces, 1.2–1.7 mm long on the adaxial surfaces; hairs of the abaxial surfaces of costules 0.3–0.6 mm long 2. *M. lanatum*

1. *Megalastrum canacae* (Holtum) Holtum, Gard. Bull. Singapore 39: 161. 1986 [1987]. Basionym: *Ctenitis canacae* Holtum, Kew Bull. 38: 128. 1983. TYPE: Mauritius. Canaca [20°24'11"S, 57°30'42"E], 1868, *H. Barkly s.n.* (holotype, K!). Figures 2M–T, 3A.

Rhizomes erect, scaly, the scales to 35 mm; fronds to 2.5 m; scales of petiole bases 10–15 × 1–1.5(–2)

mm, linear, subentire, dark brown, spreading to ascending; rachises with similar scales but often much less densely scaly; laminae to 1.2 m, bipinnate-pinnatisect at base, bipinnate-pinnatifid medially; basal pinnae 25–50 cm, the stalks to 2 cm, inequilateral, the pinnules on the acroscopic side slightly reduced toward pinna bases, the 2 or 3 first basiscopic pinnules with lobes pinnatifid and obtuse to rounded apices; pinna rachises abaxially puberulent and $\pm$ densely glandular, the hairs erect, 0.2–0.5 mm, 3- to 5-celled, the glands spherical, sessile, ca. 0.1 mm diam., 1-celled, scaly, the scales 4–7(–10) $\times$ 0.3–0.5(–1) mm, linear, entire, flat (nonbullate), dark brown, adaxially densely pubescent, the hairs spreading, 0.8–1.2 mm, 5- to 7-celled, septate, nonglandular; costules abaxially puberulent, the hairs spreading to somewhat antrorse, 0.1–0.4 mm, 1- to 3-celled, glands like those on pinna rachises but fewer, scaly, the scales 1.5–3.5 $\times$ 0.2–0.4 mm, flat, entire, brown, adaxially pubescent, the hairs antrorse, 0.6–1 mm, 5- to 7-celled, eglandular, septate; laminar tissue between veins glabrous on both surfaces, abaxially sparsely glandular, the glands spherical, sessile; veins to 8 pairs per pinnule lobe, visible on both surfaces, ending before laminar margins in enlarged clavate tips, as conspicuous hydathodes, abaxially sparsely glandular and puberulent, the hairs 0.1–0.4 mm, 2- or 3-celled, adaxially eglandular, puberulent to glabrous, the hairs ca. 0.3–0.5 mm, 3- to 5-celled; laminar margins sparsely ciliate, the hairs ca. 0.3–0.5 mm, 2- or 3-celled; indusia present, persistent (rarely deciduous), circular, 0.3–0.5 mm, pubescent, the hairs 0.1–0.3 mm, 1- or 2-celled, also present on the margins; spores monolet, the perispores fenestrate with short spines on arms between the fenestrae.

Distribution and ecology. *Megalastrum canacae* is a terrestrial fern, found in shady stations of wet mesotherm forests, in ravines, at about 1200 m. The taxon is rare in Mauritius and La Réunion. It is either very rare or possibly now extinct in Mauritius, where it was last collected in 1985 by W. Strahm (collection number 20906), who wrote on the herbarium label “only a few individuals, rare.” The only other known locality in Mauritius is Trou Kanaka, where it has not been collected since 1868, although it was searched for at this locality in the early 1980s (Holttum, 1983).

Etymology. The specific epithet *canacae* refers to the crater Kanaka (or Canaca) in Mauritius, where the type specimen was collected.

Discussion. *Megalastrum canacae* is the only species of the genus in the Paletropics with glabrous

laminar tissue between veins on both faces. Other useful characters for distinguishing this species are the numerous dark brown scales that extend from the petiole to the rachis, the antrorse hairs on the adaxial surfaces of the costules and veins, and the persistent indusia.

Contrary to Holttum’s statement (1983), the basal basiscopic pinnules of basal pinnae are not necessarily significantly shorter than those next to them. Thus, examining additional specimens, especially recent collections from La Réunion, this character does not appear to distinguish the species. The density of spherical glands observed on the abaxial surfaces can vary among specimens from almost none (*E. Grangaud 4, 5, 1824*) to many (*H. Barkly s.n.*, the holotype). With few exceptions where indusia are extremely reduced and present on only a few pinnules (*E. Grangaud 5* and *1243bis*), indusia are conspicuous, even when dried and shriveled on dried specimens.

Additional specimens examined. MAURITIUS. s. loc., s.d., *W. Bojer s.n.* (K); s. loc., 1871, *W. Cattell s.n.* (NY); s. loc., s.d., s. coll. 787 (P); s. loc., s.d., s. coll. (K); s. loc., 1827, *F. W. Sieber 36* (BR, HBG, HBG photo at MO and K, MO, NY, P); s. loc., 1827, *F. W. Sieber s.n.* (P); Brise Fer, [20°22’35”S, 57°25’28”E], *W. Strahm 20906* (K). LA RÉUNION. s. loc., 1875, *I. B. Balfour s.n.* (K); s. loc., s.d., *J. Potier s.n.* (P). **Saint-Benoît:** Plaine des Palmistes, ravine du Grand Bras Piton, [21°7’0”S, 55°38’0”E], *E. Grangaud 1547* (P). **Saint-Pierre:** Le Dimitile, sentier de la Grande Jument, [21°10’0”S, 55°29’0”E], *E. Grangaud 1243bis* (P); Entre-Deux, Le Dimitile, piste 4 $\times$ 4 de la Chapelle, petite ravine dans la partie proche de la piste, [21°10’0”S, 55°29’0”E], *E. Grangaud & M.-F. Grangaud 4, 5, 1824* (P).

2. *Megalastrum lanatum* (Fée) Holttum, Gard. Bull. Singapore 39: 161. 1986 [1987]. Basionym: *Phegopteris lanata* Fée, Mem. Foug., Gen. Fil. 246. 1850. *Ctenitis lanata* (Fée) Holttum, Kew Bull. 38: 129, 130. 1983. TYPE: La Réunion. s.d., *De Montbrison s.n.* (holotype, P 00483090!). Figures 2G–L, 3B.

Phegopteris montbrisoniana Fée, Mem. Foug., Gen. Fil. 247. 1850. TYPE: “Habitat in insula Borboniâ” [La Réunion], s.d., *De Montbrison s.n.* (holotype, P 00610771!).

Aspidium oppositum Kaulf. ex Spreng. var. *subglandulosum* Mett. ex Kuhn, Filic. Afr. 138. 1868, nom. nud.

Rhizomes short-creeping, scaly, the scales to 20 mm; fronds to 2 m; scales at petiole bases 8–11 $\times$ 0.8–2(–3) mm, linear, subentire, dark brown, spreading; rachises with a few, similar but smaller scales in the proximal half; laminae to 1.2 m, deltate, bipinnate-pinnatifid at base and medially; basal pinnae 18–30 cm, the stalks to 1.5 cm, inequilateral, the pinnules on the acroscopic side slightly reduced toward the base of the pinna, the first basiscopic

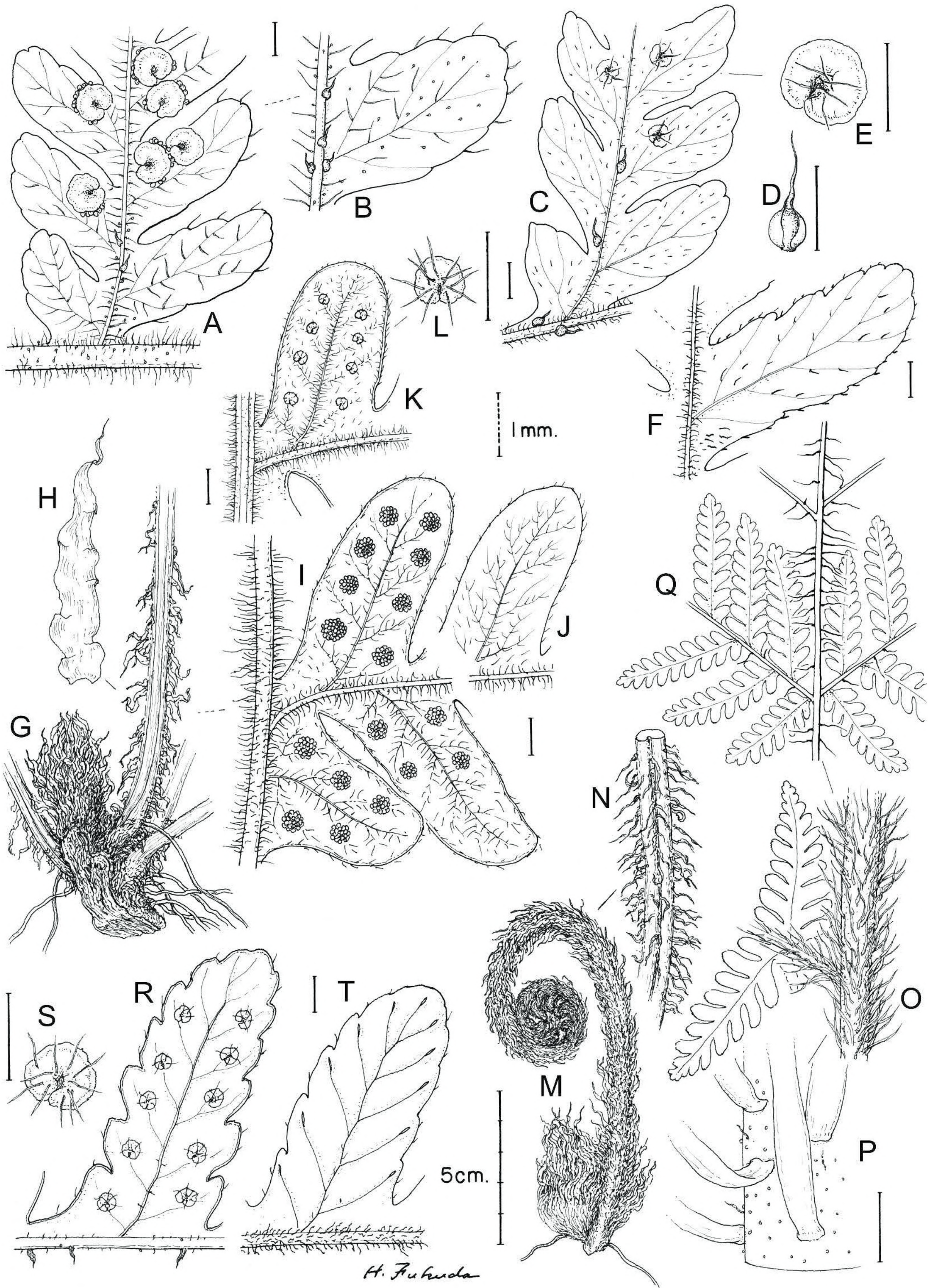


Figure 2. Indument characteristics of the three Paletropical species of *Megalastrum*. A–F. *M. lanuginosum*. —A. Abaxial surface of pinnule. —B. Abaxial surface of lobe. —C. Abaxial surface of pinnule. —D. Bullate scale from abaxial surface of costule. —E. Indusium. —F. Adaxial surface of lobe. Note veins extending to laminar margin. G–L. *M. lanatum*. —G. Rhizome apex. —H. Rhizome scale. —I. Abaxial surface of pinnule. —J. Abaxial surface of lobe. —K. Abaxial surface of lobe. —L. Indusium. M–T. *M. canacae*. —M. Crozier. —N. Petiole base. —O. Rachis and basal pinnules. —P. Rachis with scale bases and sessile glands. —Q. Adaxial medial pinnae. —R. Abaxial surface of lobe. —S. Indusium. —T. Adaxial

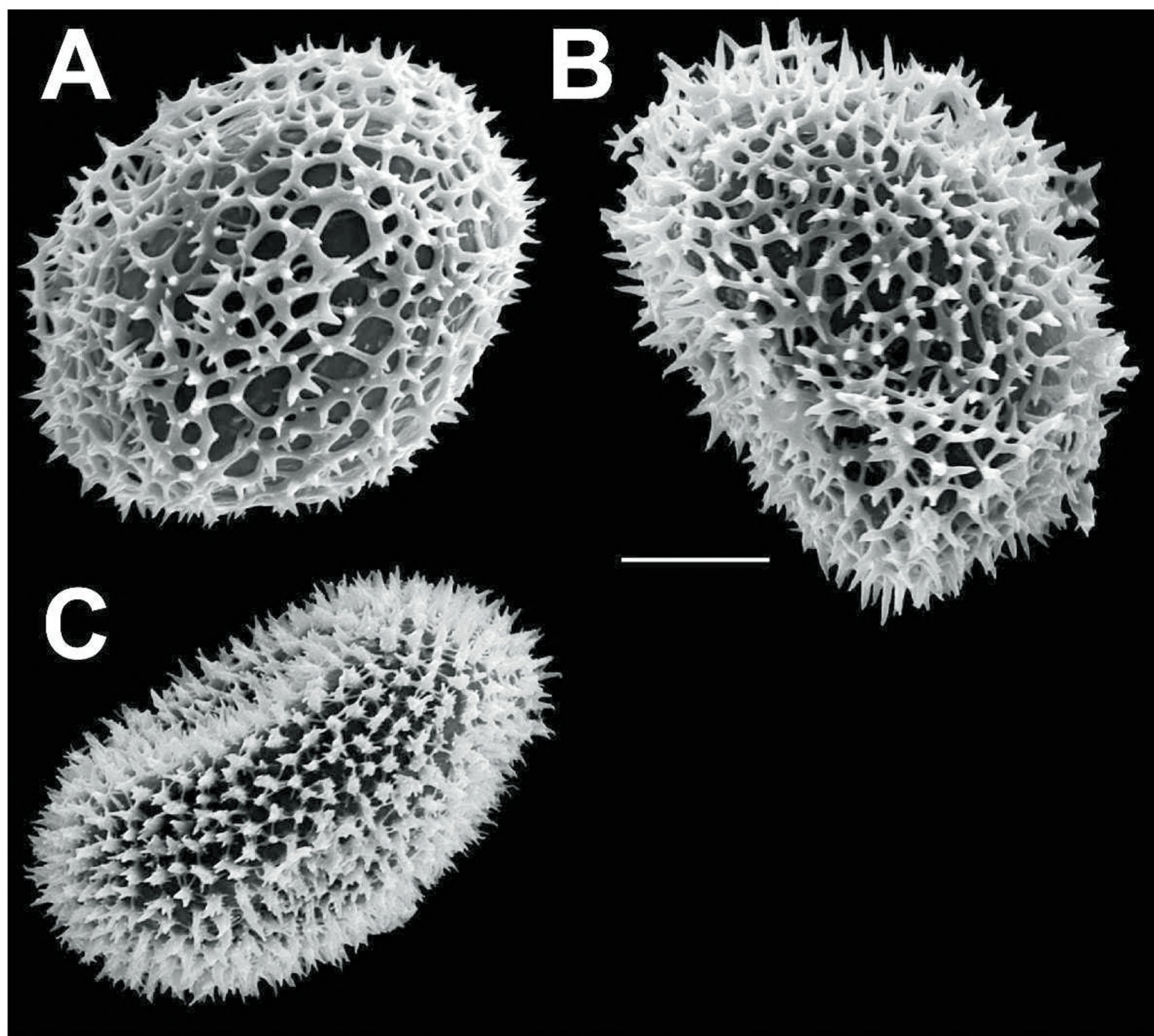


Figure 3. Spores of *Megalastrum*. —A. *M. canacae*, I. B. Balfour s.n. (K). —B. *M. lanatum*, E. Grangaud 7 (P) from La Réunion. —C. *M. lanuginosum*, L. E. Taylor 754 (NY). Scale bar = 10 μ m.

pinnules with lobes lobulate, other pinnules with lobes crenate to subentire toward the apex of the pinna; pinna rachises abaxially pubescent, eglandular, the hairs erect, 0.5–1.2 mm, to 6-celled, scaly, the scales $2\text{--}4 \times 0.2\text{--}0.5$ mm, linear, entire, flat (nonbullate), dark brown, adaxially densely pubescent, the hairs erect, 1.2–1.7 mm, 6- to 8-celled, septate, nonglandular; costules abaxially puberulent, eglandular, the hairs spreading to erect, 0.3–0.6 mm, 3- to 5-celled, scaly, the scales $0.3\text{--}0.7 \times \text{ca. } 0.2$ mm, flat, entire, adaxially densely pubescent, the hairs erect to spreading, 0.6–1(–1.5) mm, 5- to 7-celled, eglandular, septate; laminar tissue between veins pubescent on both surfaces, abaxially rarely glandular, the glands spherical, sessile, clear or yellowish translucent, to 0.1 mm diam., hairs erect to spreading on both surfaces, 0.3–0.6 mm, 3- to 5-celled; veins to 7 pairs per pinnule lobe, visible on both surfaces, ending before laminar margins in enlarged clavate tips as conspicuous hydathodes, pubescent with hairs like those of the laminar tissue;

laminar margins sparsely ciliate, the hairs similar to those of the laminar surfaces; indusia absent, or if present (rarely), reduced, pubescent, pale brown, dull, to 0.5 mm diam., hairs mostly on the margins, ca. 0.5 mm; spores monolet, the perispores fenestrate with short spines on arms between the fenestrae.

Distribution and ecology. *Megalastrum lanatum* is endemic to La Réunion, where it is terrestrial in wet forests, 750–1550 m. Although one specimen (*J. N. Bréon* s.n., 1834) has “Madagascar” written on it, we believe this to be an error. There is no other collection of *M. lanatum* from Madagascar, and Bréon collected *M. lanatum* in La Réunion in the same year.

Etymology. The species epithet is taken from the Latin word “lana,” meaning “wool,” referring to the conspicuous, dense, whitish pubescence evident on both faces of the laminae.

← surface of lobe. Note veins ending before the margin. Structures are drawn from the following collections: E. A. C. L. E. Schelpe 5375 (BOL) from South Africa (A); A. J. Whellan 219 (NY) from South Africa (B); R. B. Faden et al. 72/190 (BOL) from Kenya (C–F); F. Badré 914bis (P) from La Réunion (G–K); L. H. Boivin 884 (P) from La Réunion (L, M); E. Grangaud 4 (P) from La Réunion (N, O); H. Barkly s.n. (K) from Mauritius (P–R); F. W. Sieber 36 (P) from Mauritius (S, T). Scale bars: A–M, P–T = 1 mm; N, O = 5 cm.

Discussion. *Megalastrum lanatum* differs from *M. canacae* by the laminae between veins pubescent on both surfaces and longer hairs on the pinna rachises and abaxial surfaces of costules. The lack of indusia distinguishes *M. lanatum* from the other two species of the Old World; however, small indusia can be rarely found on a few specimens. Also, indusia may be present but fugacious, and thus only rarely observed. When present, indusia are very reduced, pubescent, and often almost completely hidden by sporangia, with the only evidence of their presence being the marginal hairs that exceed the sporangia.

As noted for *Megalastrum canacae*, recent observations and collections made in La Réunion demonstrate that the length of the basal basispic pinnules of basal pinnae is not necessarily shorter than the pinnules next to them, as was claimed by Holttum (1983).

Additional specimens examined. LA RÉUNION. s. loc., s.d., *I. B. Balfour* s.n. (K); s. loc., 1850, *C. Bernier* 92 (K); s. loc., s.d., *H. Blanchard* s.n. (US); s. loc., s.d., *L. H. Boivin* s.n. (P); s. loc., 1834, *J. N. Bréon* s.n. (P); s. loc., s.d., *De Montbrison* s.n. (P); s. loc., s.d., *I. ? Garnier* s.n. (BR); s. loc., s.d., *C. Gaudichaud* s.n. (P); s. loc., 1844, *J. A. I. Pancher* s.n. (K); s. loc., s.d., *J. M. C. Richard* 46 (P); s. loc., 4 Mar. 1847, s. coll. s.n. (P). **St. Benoît:** Salazie, sentier vers La Nouvelle, [21°4'0"S, 55°25'0"E], *F. Badré* 1052 (P); Salazie, [21°3'0"S, 55°30'0"E], s.d., *L. H. Boivin* 122 (BR); Petite Plaine des Palmistes, [21°8'59"S, 55°36'34"E], *T. Cadet* 4345 (K); Plaine des Palmistes, [21°7'0"S, 55°38'0"E], *M. G. De L'Isle* 429 (K, P); en limite de St. Benoît et Salazie, Forêt de Bélouve, sentier du Mazerin, en bas de pente du coteau Monique, [21°2'0"S, 55°33'0"E], *E. Grangaud et al.* 6 (P); en limite de St. Benoît et Salazie, Forêt de Bélouve, sentier du Mazerin, en bas de pente du coteau Monique, [21°2'0"S, 55°33'0"E], *E. Grangaud et al.* 7 (P), *E. Grangaud et al.* 8 (P); Bois à Hellbourg, [21°3'0"S, 55°32'0"E], 11 Sep. 1882, s. coll. s.n. (P). **St. Denis:** Bois du Boucan Launay, [20°53'0"S, 55°27'0"E], *L. H. Boivin* 814 (P); Le Boucan Launay, au dessus de l'Habitation de Mr. Valentin, [20°53'0"S, 55°27'0"E], s.d., *L. H. Boivin* 884 (P). **St. Paul:** Rte. forestière du Pic Maïdo, [21°4'36.53"S, 55°23'0.43"E], *F. Badré* 781 (P). **St. Pierre:** Cilaos, Bonnet Carré, [21°6'0"S, 55°26'0"E], *F. Badré* 914 bis (P); Cilaos, Bonnet Carré, [21°6'0"S, 55°26'0"E], *F. Badré* 914 (P); Saint Philippe, Basse Vallée, [21°20'12.44"S, 55°42'9.58"E], *F. Badré* 1001 (P); Saint Philippe, Forêt de La Mare Longue, [21°22'0"S, 55°45'0"E], *F. Badré* 1009 (P); Le Tampon, Forêt de Sainte Thérèse, pointe du Bras Creux, *E. Grangaud et al.* 1823 (1 and 2) (P); betw. St. Philippe & St. Joseph, La Vallée Heureuse, above Basse Vallée, [21°19'9.30"S, 55°41'41.12"E], *K. U. Kramer, F. Gartmann & M. Kramer* 9291a (P).

3. *Megalastrum lanuginosum* (Willd. ex Kaulf.) Holttum, Gard. Bull. Singapore 39: 161. 1986 [1987]. Basionym: *Aspidium lanuginosum* Willd. ex Kaulf., Enum. Filic. 244. 1824. *Nephrodium lanuginosum* (Willd. ex Kaulf.) Desv., Mém.

Soc. Linn. Paris 6: 262. 1827. *Lastrea lanuginosa* (Willd. ex Kaulf.) T. Moore, Index Fil. 87. 1858. *Polystichum lanuginosum* (Willd. ex Kaulf.) Keyserl., Polyp. Herb. Bunge 45. 1873. *Dryopteris lanuginosa* (Willd. ex Kaulf.) C. Chr., Index Fil. 273. 1905. *Ctenitis lanuginosa* (Willd. ex Kaulf.) Copel., Gen. Fil. 124. 1947. TYPE: Mauritius. s. loc., s.d., *L. M. A. Aubert du Petit-Thouars* s.n. (holotype, B-W 19808 [2 sheets likely representing a single specimen!]). Figures 2A–F, 3C.

Nephrodium elatum Desv., Mém. Soc. Linn. Paris 6: 262. 1827, non *Nephrodium elatum* Baker, 1874. TYPE: La Réunion. s.d., s. coll. s.n. (holotype, P 00610737!). *Aspidium catopteron* Kunze, Linnaea 10: 550. 1836. *Lastrea catoptera* (Kunze) Pappe & Rawson, Syn. Fil. Afr. Austr. 12. 1858. *Nephrodium catopteron* (Kunze) Hook., Sp. Fil. 4: 137. 1862. *Dryopteris catoptera* (Kunze) Kuntze, Revis. Gen. Pl. 2: 812. 1891. TYPE: South Africa. Koratra, "in valle rupestri umbrosa secus rivulum inter Omsamcaba et Omsamwubo et prope Koratra in sylva 500–1000 p.," 1838, *J. F. Drège* s.n. (lectotype, designated by Roux [1986: 377], BM not seen; duplicates, NY, S).

Lastrea odorata C. Presl, Tent. Pterid. 77. 1836, nom. nud. *Aspidium odoratum* Mett., Abh. Senckenberg. Naturf. Ges. 2: 399. 1858, nom. nud., non *Aspidium odoratum* Bory ex Willd., 1810.

Rhizomes massive, erect or procumbent, sometimes arborescent (resembling a small tree fern) and forming a trunk to 50(–100) cm high, 15 cm thick, scaly, the scales to 30×3 mm, linear, thin, translucent, light golden brown, papyraceous, subentire and irregularly dentate-serrulate toward the apex; fronds to 2.5 m; petiole bases subglabrous, rarely bearing a few scales similar to those on the rhizome, but smaller, to 4×0.5 mm; laminae to 1.5 m, deltate, triangular to pentagonal; blades tripinnate-pinnatifid to tripinnate-pinnatisect (rarely quadripinnate-pinnatifid) at base, bipinnate-pinnatifid or bipinnate-pinnatisect medially (rarely tripinnate-pinnatifid); basal pinnae to 100 cm, the stalks to 3.5 cm, strongly inequilateral with the basal basispic pinnules much more elongate, the most basal basispic pinnules to 35 cm, to 5 times the length of the most basal acroscopic ones, the pinnules on the acroscopic side slightly reduced toward the pinna base; pinna rachises abaxially puberulent to pubescent, eglandular, the hairs erect to spreading, 0.2–1 mm, to 8-celled, very sparsely scaly, the scales 0.5–1 $\times$ 0.2–0.3 mm, linear, entire, flat and nonbullate, dark brown to light brown, adaxially densely pubescent, the hairs erect, 0.3–1 mm long, 5- to 8-celled, septate, eglandular; costules abaxially pubescent, glandular or eglandular, the glands spherical, yellowish translucent, shiny, sessile or stalked, ca.

0.1 mm diam., 1- or 2-celled, the hairs spreading, (0.2–)0.5–1.7 mm long, 6- to 8-celled, very sparsely to abundantly scaly, the scales $0.3\text{--}1.5 \times \text{ca. } 0.3\text{--}0.5$ mm, flat to conspicuously bullate, entire, light brown, dull, rarely clathrate, adaxially pubescent, eglandular, the hairs erect to spreading, 0.5–0.7(–1.2) mm, 3- to 5-celled, septate; laminar tissue between veins from pubescent on both surfaces to subglabrous on both surfaces, abaxially eglandular or sparsely glandular, the glands like those of the costules, hairs erect to spreading, 0.2–1.2 mm, 3- to 8-celled, thicker on the adaxial surfaces; veins 3 to 5 pairs per pinnule lobe, visible on both surfaces, ending at or close to (rarely before) laminar margins (except for those veins with sori that end well before laminar margins) in enlarged clavate tips as conspicuous hydathodes, abaxially pubescent and sparsely glandular to eglandular, glands spherical, yellowish clear, shiny, sessile or stalked, ca. 0.1 mm diam., hairs erect, 0.3–1 mm, usually 4- to 6-celled, adaxially pubescent, hairs erect to spreading, 0.4–0.8 mm long, 4- to 6-celled; laminar margins ciliate, hairs similar to those on laminar tissue; sori on acroscopic branches of forked veins, indusia present and persistent, covering sporangia, orbicular-reniform, to 1.5 mm diam., dark brown, shiny, densely pubescent to glabrous, densely glandular or eglandular, glands 1- or 2-celled, yellowish, shiny, hairs to 0.7 mm, margins dull and erose; spore monolete, the perispores nonfenestrate, echinulate.

Distribution and ecology. *Megalastrum lanuginosum* has a disjunct distribution between tropical West Africa, where it is restricted to Bioko and São Tomé (one specimen—not seen—is cited from Río Muni, the continental region of Equatorial Guinea; Velayos et al., 2008), and eastern Africa and the Madagascan region, the latter including tropical East Africa, eastern South Africa, Madagascar, the Mascarene Islands (La Réunion and Mauritius), and the Comoros (Fig. 1). It is rare or perhaps extinct in the Mascarene Islands (no collection since 1925, although it was recently sought in La Réunion; E. Grangaud, pers. comm.) and rare and local in the Gulf of Guinea islands (Benl, 1991), but *M. lanuginosum* can be locally common in East Africa.

This is a terrestrial fern encountered in deep shade of evergreen forests, in swampy areas, and most frequently observed near or on banks of permanent streams, from 850 to 2150 m. *Megalastrum lanuginosum* has also been present in cloud forests, and mentioned once from a rock fissure. The taxon can resemble a small tree fern, likely to 1 m high, according to the annotation on *E. A. C. L. E. Schelpe 1689* (BOL).

Etymology. The specific epithet is taken from the Latin “lanugo,” meaning wool or down, referring to the pubescence of the leaves. Although this is the condition of most specimens of *Megalastrum lanuginosum*, some specimens are only sparsely pubescent.

Discussion. *Megalastrum lanuginosum* differs from the two endemic Mascarene species by the laminae at least tripinnate-pinnatifid at the base (rarely quadripinnate), appearing more finely dissected when compared to the bipinnate-pinnatifid laminae in *M. lanatum* and *M. canacae*. Other useful differentiating characters include the scales of the rhizomes that are light golden brown, papyraceous, with small irregular marginal teeth toward the apex, and the large, conspicuous, and persistent indusia. Leaf veins usually end at or close to (rarely before) the laminar margins, which is remarkable in the genus. Only the Neotropical *M. inaequale* (Kaulf. ex Link) A. R. Sm. & R. C. Moran shares this character.

Other morphological characters are extremely variable in *Megalastrum lanuginosum*. Although bullate scales are found only in *M. lanuginosum* and observable on almost all specimens, their density and size show great variation among specimens. Contrary to Holttum (1983), we found a few small bullate scales on Mascarene specimens (to see these scales, careful inspection with at least 10 $\times$ magnification is required on the abaxial surfaces of costules). Because numerous morphological intermediates exist, from densely to sparsely scaly costules, and from large to small bullate scales, individual species cannot be distinguished on the basis of indument. Also, the indusia vary in the presence and abundance of hairs and glands, and in hair length. We find no other character correlating with this, and therefore we interpret these variations as phenotypic plasticity within a single taxon.

Megalastrum lanuginosum varies greatly in indument, especially as to the location, abundance, and length of hairs, and these characters overlap with those of *M. lanatum*. This variation does not correlate with geography. For example, the length of hairs on pinna rachises, costules, and veins varies even within the Mascarene Islands. Most of the specimens have long hairs (exceeding 0.5 mm), whereas two specimens (*s. coll. s.n.*, in Hb. Desvaux, La Réunion, P 00610737; *J. B. G. M. Bory de St. Vincent s.n.*, Mauritius, P 00483107 and P 00477882) have shorter hairs (less than 0.4 mm). Similarly, in Bioko, the laminar tissue between the veins is glabrous in some specimens but pubescent in others.

Additional specimens examined. COMOROS. **Grande Comore:** Massif du Karthala, versant O, piste menant de

Boboni à Convalescence, 11°45'S, 43°17'E, *F. Rakoton-drainibe et al.* 6727bis (P). **Mayotte:** Forêt de Combani, [12°47'48"S, 45°9'24"E], *L. Humblot* 1289 (P); 17 Oct. 1884, *L. Humblot* 1323 (K, P).

EQUATORIAL GUINEA. Bioko: Pico, [3°35'0"N, 8°46'0"E], *G. Benl & Benl* 378 FP (P); Malabo-Pico Basile, estrada Km 12, plantacoes de cacau, [3°35'0"N, 8°46'0"E], *M. Fidalgo de Carvalho* 3564 (NY); Peak, [3°35'0"N, 8°46'0"E], *G. Mann* 349 (K); s. loc., [3°35'0"N, 8°46'0"E], 1861, *G. Mann s.n.* (K).

KENYA. Embu Distr.: Mt. Kenya SE, Irangi Forest Station, 0°21'S, 37°27'E, *R. B. Faden et al.* 72/190 (BOL, K, MO). **Kiambu Distr.:** Kikuyu Escarpment Forest (S. Aberdare Forest), Karamenu River Valley adjacent to Sasumua pipeline & Karamenu Rivers, 0°51'37"S, 36°45'15"E, *R. B. Faden et al.* 71/282 (BOL). **Meru Distr.:** Ithagune forest, rd. along base of volcanic cone Kirue, 9 mi. from Nkubu, [0°4'0"S, 37°40'0"E], *R. B. Faden et al.* 69/763 (BOL, K). **Taita Distr.:** Taita Hills, Mbololo Hill, Mraru ridge, [3°21'0"S, 38°27'0"E], *R. B. Faden et al.* 69/842 (BOL, K). **Taita-Taveta Distr.:** Ngangao Forest, [3°22'0"S, 38°20'0"E], *R. B. Faden et al.* T468 (K); Dundori ravine, 0°12'0"S, 36°16'0"E, *R. R. Schippers* 49 (WAG); Taita Hills, Ngangao Forest, 3°25'0"S, 38°20'0"E, *R. R. Schippers* 249 (WAG). **Thika Distr.:** Kieni Forest, S side, 0°51'0"S, 36°40'0"E, *R. R. Schippers* 548 (WAG).

LA RÉUNION. s. loc., 1925, *G. Carles s.n.* (P); s. loc., s.d., s. coll. s.n. (P); s. loc., s.d., s. coll. s.n., (P-Desvaux).

MADAGASCAR. Antananarivo: Tsinjoarivo, Forêt d'Ankilahila à 19.2 km au SE de Tsinjoarivo, le long de la rivière d'Andrindimbolo, 19°42'24"S, 47°50'6"E, *G. Borie* 554 (P, TEF); Ankazobe, Manankazo, Réserve spec. d'Ambositantely, ca. 8 km au NO d'Ankazobe, 18°10'S, 47°17'E, *F. Rakotondrainibe* 419 (P, TEF); Anjozorobe, Forêt d'Andranomay, 2 km au NNE d'Andranomay, 13 km au SE d'Anjozorobe, 18°28'48"S, 47°57'18"E, *F. Rakotondrainibe* 3720 (MO, P); Ankazobe/Manankazo, RS d'Ambositantely, partie méridionale de la réserve, 18°13'S, 47°17'E, *F. Rakotondrainibe & Randriambololona* 4461 (P). **Antsiranana:** Andapa, Befingotra, RS d'Anjanaharibesud, sur le versant SE, à 6.5 km au SSO de Befingotra, 14°45'18"S, 49°30'18"E, *F. Rakotondrainibe & Raharimalala* 2194 (P, TEF). **Fianarantsoa:** Ambalavao, Ambatomboay, RNI d'Andringitra versant Est, 40 km S d'Ambalavao, sur les berges d'un affluent de la rivière Sahavatoy, 22°13'22"S, 46°58'18"E, *F. Rakotondrainibe* 2695 (P, TEF); Ambalavao, RS d'Ivohibe, à 8 km à l'Est du village d'Ivohibe, 22°29'0"S, 46°58'6"E, *F. Rakotondrainibe & Randriambololona* 4176 (P); Ranomafana-Ifanadiana, PN de Ranomafana, forêt de Vatoharanana, à 4 km au SO du village de Ranomafana, 21°17'24"S, 47°26'00"E, *F. Rakotondrainibe & Randriambololona* 5919 (P). **Mahajanga:** Forêt du Bangolava, 120 km O de Tsiromandioly vers Morafenobe, [16°5'0"S, 47°18'0"E], *G. Cremers* 3268 (P); near Andribe, forest remnant at high plateau, 17°30'S, 47°0'E, 1500 m, *H. van der Werff & McPherson* 13545 (MO, UC). **Toamasina:** Ambatondrazaka, Ankaroka, [19°7'0"S, 44°44'0"E], *G. M. Cours* 209 (P); Moramanga, Forêt de Sandrangato, au S de Moramanga, [19°10'0"S, 48°15'0"E], *R. Decary* 17837 (P); Grande forêt d'Analamazoatra, [18°56'0"S, 48°25'0"E], *C. Alleizette* 19 (P); Mandraka, [18°55'0"S, 47°56'0"E], *C. Alleizette* 77 (P), *C. Alleizette* 171 (P), *C. Alleizette* 182 (P); Andovoranto, Moramanga, forêt d'Analamazotra [18°56'0"S, 48°25'0"E], *R. Viguier & Humbert* 869 (P). **Toliara:** Massif du Kalambatitra, Mt. Kalambatritra et ses abords, [23°22'0"S, 46°29'0"E], *H.*

Humbert 11905 (P); Massif du Kalambatritra, Mt. Analatsitendrika, [23°22'0"S, 46°29'0"E], *H. Humbert* 11944 (P, TAN); Tolanaro, Eminiminy, parcelle 1, RNI n°11 d'Andohahela, versant E et sommet du Trafon'omby, 13.5 km au NW d'Eminiminy, Camp 3, 24°35'4"S, 46°44'8"E, *F. Rakotondrainibe* 3080 (P); Tolanaro, Eminiminy, parcelle 1, RNI n°11 d'Andohahela, versant E et sommet du Trafon'omby, Camp 4, 15 km au NW du village d'Eminiminy, [24°33'0"S, 46°43'0"E], *F. Rakotondrainibe* 3128 (P); Fivondronana, Betroka, Ivahona, Voromiantsa, forêt dense de Befarafara, Kalambatritra, 23°25'2"S, 46°27'5"E, *R. Razakamalala et al.* 1992 (P).

MALAWI. Kota-Kota Distr.: Nchisi Mtn., [13°19'0"S, 34°3'0"E], *L. J. Brass* 17040 (K, MO, NY, US); Cholo Mtn., [16°5'0"S, 35°3'0"E], *L. J. Brass* 17757 (K, MO, NY, US); Nchisi forest, [13°19'0"S, 34°3'0"E], *J. D. Chapman* 836 (BOL). **Thyolo Distr.:** Mt. Thyolo, [16°10'0"S, 35°10'0"E], *J. P. Roux* 2916 (NBG).

MAURITIUS. Escalier woods, s.d., *H. Barkly s.n.* (K); des grands bois du Milieu, [20°17'12"S, 57°35'3"E], Oct. 1801, *J. B. G. M. Bory de St Vincent s.n.* (P); s. loc., 1871, *W. Cattell s.n.* (NY); s. loc., s. coll. 72 (P); s. loc., *F. W. Sieber* 48 (BR, K, MO, P, S); s. loc. [possibly from Mauritius], s.d., *L. M. A. Thouars s.n.* (P).

MOZAMBIQUE. Bandula Mtns., [19°0'42"S, 33°8'36"E], *N. C. Chase* 6596 (BOL, K). **Manica/Sofala:** Yaegersberg, Cavuso, [19°4'32"S, 33°55'34"E], *E. A. C. L. E. Schelpe* 5621 (BOL, NBG). **Zambezia Prov.:** Namuli, Makua country, [15°22'27"S, 37°2'26"E], s.d., *J. T. Last s.n.* (K); Morrumbala, [16°59'0"S, 35°38'0"E], *E. P. Luja* 347 (BR); Morrumbala, [16°59'0"S, 35°38'0"E], *E. P. Luja* 348 (BR, P).

SÃO TOMÉ ISLAND. s. loc., [0°16'0"N, 6°33'0"E], 1861, *G. Mann s.n.* (K).

SOUTH AFRICA. In valle rupestris umbrosa secus rivulum inter Omsamcaba et Omsamwubo et prope Koratra in sylva, 1844, *J. Drège s.n.* (NY); Westfalia state, s. loc., *J. C. Scheepers* 436 (PRE); s. loc., s.d., *D. Brown s.n.* (BOL); s. loc., s.d., *J. Drège s.n.* (K). **Eastern Cape:** Transkei, Tsolo, Ntywenka, [30°44'0"S, 28°45'0"E], *S. Cawe* 735 (BOL); Transkei, Port St. Johns, [31°36'21"S, 29°31'11"E], *A. G. M. McLoughlin* 785D (BOL). **Kwazulu-Natal:** s. loc., [29°0'0"S, 30°0'0"E], *Beivsher?* 3/88 (US) [29°0'0"S, 30°0'0"E], *J. Buchanan* 138 (NY); s. loc., [29°0'0"S, 30°0'0"E], *J. Buchanan* 558 (US); s. loc., [29°0'0"S, 30°0'0"E], *J. Buchanan* 559 (US); Lions River, Dargle, [29°29'0"S, 30°10'0"E], *E. Esterhuysen* 26199 (BOL, US); Mowbray' Ahrens, [29°4'0"S, 30°46'0"E], *B. S. Fisher* 947 (BOL); s. loc., [29°0'0"S, 30°0'0"E], s.d., *R. J. Garden s.n.* (K); s. loc., [29°0'0"S, 30°0'0"E], *W. T. Gerrard* 1933 (K); s. loc., [29°0'0"S, 30°0'0"E], *W. T. Gerrard* 1953 (GH); s. loc., [29°0'0"S, 30°0'0"E], *M. J. M. Ken* 52 (K); S Natal, Weza State Forest, Mpetsheni Forest, [30°36'0"S, 29°40'0"E], *A. Nicholas & Marais* 1674 (MO, PRE); Natal, Dlinza Forest Res., Eshowe, [28°53'18"S, 31°26'54"E], *B. S. Parris & Croxall* 7273 (K), *B. S. Parris & Croxall* 7276 (K); Lidgetton, [29°27'0"S, 30°6'0"E], *A. Roberts* 970c (PRE); Khandla forest, Zululand, [28°0'0"S, 32°0'0"E], *E. A. C. L. E. Schelpe* 1689 (BOL); Ngotsche, Ngome forest, [27°52'0"S, 31°24'0"E], *E. A. C. L. E. Schelpe* 6220 (BOL, US); Kranskop, [28°28'0"S, 29°22'0"E], 13 Apr. 1980, *E. J. van Jaarsveld* 2830 (NBG); 10 km from Kwasizabantu toward Mapumulo, S slope, [29°11'0"S, 31°3'0"E], *E. J. van Jaarsveld* 5104 (K, MO, PRE, S); Kranskop, [28°55'0"S, 30°57'0"E], *E. J. van Jaarsveld* 5116 (PRE); s. loc., [29°0'0"S, 30°0'0"E], s.d., *Wood? s.n.* (US); Inanda,

[29°37'0"S, 30°56'0"E], s.d., *M. Wood s.n.* (MICH, UC). **Limpopo:** Transvaal, Magoebaskloof, [23°51'0"S, 30°01'0"E], *N. C. Anthony 2330* (NBG); Transvaal, Broederstroom & Woodl. Reserve, [23°46'0"S, 30°1'0"E], *A. F. Braithwaite 258* (BOL); NE Transvaal, Grootbos', woodbush Forest Res., Tzaneen, [23°49'0"S, 30°10'0"E], *J. E. Burrows 3244* (BOL); Transvaal, Pilgrim Rest distr., Mount Sheba Nature Res., [24°56'0"S, 30°43'0"E], *J. Jacobsen 4432* (PRE); Transvaal, Mac Mac Natuurreservaat, [24°59'0"S, 30°50'0"E], *J. P. Kluge 2257* (PRE); New Agatha Forest Res., [24°01'0"S, 30°04'0"E], *P. J. Muller & J. C. Scheepers 101* (WAG); Transvaal, Houtbosch, [24°51'0"S, 30°57'0"E], *A. Rehmann 5601* (K); Woodbush Forest Res., [23°46'0"S, 30°4'0"E], *J. P. Roux 2330* (NBG); Transvaal, Entabeni, Zoutpansberg, [22°58'0"S, 29°45'0"E], *E. A. C. L. E. Schelpe 6011* (BOL, US); Transvaal, Entabeni, [22°58'0"S, 29°45'0"E], *L. E. Taylor 754* (NY, UC). **Western Cape:** Cape, [33°58'0"S, 18°25'0"E], s.d., *J. Bowie s.n.* (K); Austral Africa, *W. J. Burchell 5436* (GH, K, NY, S); ca. 1 km W of Bloukrans River Bridge, Bloukrans Pass, [33°58'02.17"S, 23°38'42.62"E], *J. E. Burrows 1453* (BOL, NBG); Cape, [33°58'0"S, 18°25'0"E], s. coll. 775 (GH); s. loc., s.d., s. coll. s.n. (NY); Cape, Lusikisiki, Egoso forest above Magwa waterfall, [31°26'0"S, 29°38'0"E], *Venter & Vorster 81* (MO, PRE, US).

TANZANIA. Iringa: Ludewa Distr., forests around Milo village, [9°53'0"S, 34°39'0"E], *J. Lovett et al. 13685* (AAU). **Morogoro:** Uluguru Mtns., Mwere valley, [7°10'0"S, 37°40'0"E], *R. B. Faden et al. 70/585* (K); N. Uluguru Forest Res., Lupanga Peak, E side, [6°52'0"S, 37°43'0"E], 1991, *J. B. Hall s.n.* (K); Kanga Mtn., N Nguru, 6°0'S, 37°43'E, *J. Lovett & D. W. Thomas 2791* (MO); Kilombero Distr., Mwanihana Forest Res. above Sanje village, 7°50'S, 36°55'E, *D. W. Thomas 3862* (MO, P). **Tanga:** Lushoto Distr., Shume-Magamba Forest Res., [4°40'0"S, 38°15'0"E], *C. M. Kisenia 459* (K).

ZIMBABWE. s. loc., s.d., *J. Drège s.n.* (MO). **Melsetter Distr. [Chimanmani]:** [19°53'0"S, 32°49'0"E], *N. C. Chase 4833* (MO, PRE); Muchira River, S of Mont Peni, [19°59'0"S, 32°54'0"E], *B. Goldsmith 27/73* (BOL, MO, P); Gungunyana Forest, [20°24'0"S, 32°43'0"E], *A. J. Whellan 219* (NY). **Mutare Distr.:** Vumba Mtns. Distr., stream on S slopes of Bungo forest, [19°5'0"S, 32°45'0"E], *J. E. Burrows 1678* (BOL); Umtali Distr., Vumba, [19°5'0"S, 32°45'0"E], *N. C. Chase 5140* (GH, MO, NBR, PRE, S, UC), *N. C. Chase 5703* (BOL); Vumba Mtns. Distr., s. loc., [19°5'0"S, 32°45'0"E], *E. A. C. L. E. Schelpe 5375* (BOL, MO, P, PRE).

EXCLUDED SPECIES

The following taxa have been previously ascribed to *Megalastrum*. However, they do not have the characteristic of the venation and cutting of *Megalastrum*: the basal basiscopic vein on the distal pinnules arises from the costules (not from the costa, as in *Megalastrum*). Furthermore, hairs present on the adaxial surfaces of the axes differ from those of *Megalastrum* in having cells apparently twisted relative to each other when dried. Finally, the following taxa have unicellular, cylindrical, glandular hairs on the stalks of the sporangia. All these

morphological characters define the following taxa as belonging in *Ctenitis*.

Ctenitis exaggerata (Baker) Ching, Sunyatsenia 5: 250. 1940. Basionym: *Nephrodium crinitum* (Poir.) Desv. var. *exaggeratum* Baker, Ann. Bot. (Oxford) 5: 319. 1892. *Dryopteris exaggerata* (Baker) C. Chr., Dansk Bot. Ark. 7: 60, t. 16, f. 4–7. 1932. *Megalastrum exaggeratum* (Baker) Holttum, Gard. Bull. Singapore 39: 161. 1986 [1987]. TYPE: Madagascar. Antananarivo, s.d., *W. Pool s.n.* (holotype, K 000351137!).

Ctenitis magna (Baker) Tardieu, in Humbert, Fl. Madagasc. 5: 344. 1958. Basionym: *Nephrodium magnum* Baker, J. Bot. 22: 142. 1884. *Dryopteris magna* (Baker) C. Chr., Index Fil. 276. 1905. *Megalastrum magnum* (Baker) Holttum, Gard. Bull. Singapore 39: 161. 1986 [1987]. TYPE: Madagascar. s.d., *L. Humblot 265* (holotype, K 000351140!; isotypes, K 000351141!, P 00483091!, P 00483092!, P 00483093!, P 00610798!).

Polypodium baronii Baker, J. Linn. Soc., Bot. 22: 535. 1887, as "*baroni.*" *Dryopteris baronii* (Baker) C. Chr., Index Fil. 254. 1905. TYPE: Madagascar. s.d., *R. Baron 3920* (holotype, K 000351138!, K 000351139!).

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 Cadet, T. 4345 (2); Caue, S. 735 (3); Chapman, J. D. 836 (3); Chase, N. C. 4833, 5140, 5703, 6596 (3); Cours, M. G. 209 (3); Cremers, G. 3268 (3).
 De L'Isle, M. G. 429 (2); Decary, R. 17837 (3).
 Esterhuysen, E. 26199 (3).
 Faden, R. B. 69/763, 69/842, 70/585, 71/282, 72/190, T468 (3); Fidalgo de Carvalho, M. 3564 (3); Fisher, B. S. 947 (3).
 Gerrard, W. T. 1933, 1953 (3); Goldsmith, B. 27/73 (3); Grangaud, E. 1243bis, 1547, 1824, 4, 5 (1); 6, 7, 8, 1823–1, 1823–2 (2).
 Humbert, H. 11905, 11944 (3); Humblot, L. 1289, 1323 (3).
 Jacobsen, J. 4432 (3).
 Ken, M. J. M. 52 (3); Kisená, C. M. 459 (3); Kluge, J. P. 2257 (3); Kramer, K. U. 9291a (2).
 Lovett, J. 2791, 13685 (3); Luja, E. P. 347, 348 (3).
 McLoughlin, A. G. M. 785D (3); Muller, P. J. 101 (3).
 Nicholas, A. 1674 (3).
 Parris, B. S. 7273, 7276 (3).
 Rakotondrainibe, F. 419, 2194, 2695, 3080, 3128, 3720, 4176, 4461, 5919, 6727bis (3); Razakamalala, R. 1992 (3); Rehmann, A. 5601 (3); Richard, J. M. C. 46 (2); Roberts, A. 970c (3); Roux, J. P. 2330, 2916, 3414 (3).
 Scheepers, J. C. 436 (3); Schelpe, E. A. C. L. E. 1689, 5375, 5621, 6011, 6220 (3); Schippers, R. R. 49, 249, 548 (3); Sieber, F. W. 36 (1), 48 (3); Strahm, W. 20906 (1).
 Taylor, L. E. 754 (3); Thomas, D. W. 3862 (3).
 van der Werff, H. 13545 (3); van Jaarsveld, E. J. 2830, 5104, 5116 (3); Venter 81 (3); Viguier, R. 869 (3).
 Whellan, A. J. 219 (3).
- APPENDIX 1. Index to collections. Each specimen is cited by the first collector, listed alphabetically by the first author's last name. The numbers in parentheses refer to the accepted species number in the taxonomic treatment.
- Alleizette*, C. 19, 77, 171, 182 (3); *Anthony*, N. C. 2330 (3).
Badré, F. 781, 914, 914bis, 1001, 1009, 1052 (2); *Beivsher?* 3/88 (3); *Benl*, G. 378 FP (3); *Bernier*, C. 92 (2); *Boivin*, L. H. 122, 814, 884 (2); *Borie*, G. 554 (3); *Braithwaite*,